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Drought-Stress Effects on Branch and Mainstem Seed Yield and Yield Components of Determinate Soybean

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ABSTRACT

A better understanding of how drought stress affects soybean [*Glycine max* (L.) Merr.] seed-yield determination would aid in the development of improved cultivars for the southeastern Coastal Plain and better production systems aimed at ameliorating the effects of drought stress. The objective of this field study was to examine the effects of drought stress on both soybean branch vegetative growth and the distribution of seed yield and yield components between the main stem and branches. Soybean was grown on an Eunola loamy sand in 1998 and 1999 with three levels of drought-stress treatment: (i) irrigation and no deep tillage, (ii) deep tillage but no irrigation, and (iii) no deep tillage or irrigation. Total seed yield, branch seed yield, and the percentage of total seed yield on the branches were highest with irrigation, followed by the in-row subsoiled/no deep tillage treatment and the no irrigation/no deep tillage treatment. Drought-stress treatment had no effect on mainstem seed yield. Branch seed number per square meter was highly correlated with branch seed yield ($r = 0.994$; $P < 0.0001$) and total seed yield ($r = 0.989$; $P < 0.01$) over both years and all levels of drought-stress treatment. A close relationship was found between branch seed number per square meter and branch dry weight at harvest maturity ($r = 0.963$; $P < 0.05$), final branch length per square meter ($r = 0.994$; $P < 0.05$), and final branch number per square meter ($r = 0.995$; $P < 0.05$). Most branch growth occurred between initial flowering and the beginning of seed fill. Less association was found between individual seed weight and seed yield from the mainstem or branch fractions. These data indicate that drought stress occurring between initial flowering and seed fill decreases total seed yield primarily by reducing branch vegetative growth, which reduces branch seed number and branch seed yield.

DROUGHT STRESS is a persistent problem with row crop production on the southeastern Coastal Plain because most Ap soil horizons are coarse-textured and have a low water-retention capacity. The severity of drought stress in this region is often increased by the occurrence of a soil tillage pan found in the Ap soil horizon, a naturally forming soil hardpan (E soil horizon) located just above the clay subsoil, or both (NeSmith et al., 1987). Irrigation and deep tillage are commonly used by Coastal Plain farmers to avoid the development of severe drought stress during the growing season. Deep tillage prior to planting allows faster and deeper root growth, thereby increasing the amount of soil water available to the crop (Busscher et al., 1986; Frederick et al., 1998).

Seed yield of determinate soybean is produced on both the mainstem and the branches originating from mainstem nodes (Board, 1987). Branch initiation usually occurs first at the cotyledonary node prior to Growth Stage V2 (Fehr et al., 1971), followed by branch initiation at the unifoliolate node between Growth Stages V2 and V6 (Acock and Acock, 1987). However, most branch vegetative growth does not occur until between Growth Stage R1 (initial flowering on main stem) and initial seed fill (Egli et al., 1985; Board and Settimi, 1986). A majority of the seed yield of determinate soybean is produced on these branches originating from the main stem (Board, 1987). Unfavorable growing conditions, such as late planting, excessive soil water, and high plant populations, reduce soybean seed yield primarily by reducing branch growth and branch seed yield per plant (Board et al., 1990; Frederick et al., 1998; Linkemer et al., 1998; Ramseur et al., 1984b). Stresses that reduce crop growth rate between Growth Stages R1 and R5 result in the greatest seed-yield decreases (Board and Harville, 1998; Board and Tan, 1995; Linkemer et al., 1998). These results indicate that branch seed yield of determinate soybean is dependent on the amount of branch vegetative growth that occurs during the flowering and pod formation stages of development.

Less is known about the effects of drought stress on soybean branch growth and branch seed yield or how drought stress affects the distribution of seed yield between the main stem and branches. Ramseur et al. (1984a,b) reported that, for the determinate cultivar Braxton, most seed yield was located on branches originating from lower mainstem nodes and that increases in seed yield with irrigation were due to increases in the number of seeds per square meter and seed weight on both the mainstem and branch fractions. Full-season irrigation and irrigation beginning at initial flowering had the same effect on seed yield in their study, suggesting that the major factors affecting seed-yield increases with irrigation do not come into effect until near initial flowering. Results from the above studies suggest environmental factors that decrease crop growth rate between Growth Stages R1 and R5 reduce total seed yield by reducing branch growth. Therefore, we hypoth-

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esized that drought stress between flowering and early seed fill has a greater effect on branch seed yield than mainstem seed yield due to the negative effects of drought stress on branch growth. The objectives of this study were (i) to examine effects of drought stress on the relationship between branch vegetative growth and branch seed yield and (ii) to identify how drought stress affects the distribution of seed yield and yield components between the main stem and branches.

MATERIALS AND METHODS

Site Description, Cultural Practices, and Treatment Application

Full-season soybean (cv. Northrup King Coker S73-Z5 in 1998 and Motte in 1999)[1] was grown in 1998 and 1999 at the Pee Dee Research and Education Center located near Florence, SC. The experiment was conducted on an Eunola loamy sand (fine-loamy, siliceous, thermic, Aquic Hapludults) using adjacent experimental sites that were rotated with cotton (*Gossypium hirsutum* L.) in both years (Camp et al., 1999). Coker S73-Z5 (a Maturity Group VII determinate cultivar) and Motte (a Maturity Group VIII determinate cultivar) were selected for this study because of their potential for high yield and good disease resistance (Palmer, 1999).

Treatment arrangement and methods of irrigation application have previously been described in detail when the site was used for research on doublecropped soybean (Camp et al., 1999). For the study reported here, full-season soybean was grown under different subsurface drip irrigation tube spacings and nonirrigated conditions. Whole plants were sampled from the following levels of drought-stress treatment: (i) the subsurface drip irrigation tubes (polyethylene) were spaced 1 m apart and the plots were not deep tilled, (ii) no irrigation water was applied (rainfed only) and the plots were in-row subsoiled every 1 m to a depth of 38 cm before planting, and (iii) no irrigation water was applied and no deep tillage conducted. A four shanked Kelly in-row subsoiling unit (Kelly Mfg. Co., Tifton, GA) was used to deep till the plots assigned to be subsoiled. All plots were planted with no surface tillage on Days 139 (19 May) and 138 (18 May) of the year in 1998 and 1999, respectively. Seeds were planted at a rate of four seeds per 30 cm of row with a John Deere 750 no-till drill (Deere and Co., Moline, IL) having a row spacing of 19 cm. Experimental plots were 15 m long and 8 m wide. Rows were oriented in a north-south direction and planted perpendicular to the irrigation tubes and subsoil slits. Soil fertility and weed control practices were conducted according to Clemson University Cooperative Extension Service recommendations.

Subsurface drip irrigation tubes were located 30 cm below the soil surface in the irrigated plots. Irrigation was applied when tensiometers placed at a depth of 23 cm averaged −0.30 MPa. Dates of irrigation in 1998 and 1999 are shown in Fig. 1. Irrigation was applied 28 times in 1998 and 27 times in 1999. Six millimeters of water were applied on each irrigation date.

Parameters Evaluated

Branch number per square meter and branch length per square meter were determined at Growth Stage R1 (initial flowering) and two weeks after Growth Stage R5 (initial seed fill) in 1999. Branch growth had terminated by 2 wk after Growth Stage R5, as has been reported by others (Board and Settimi, 1986; Egli et al., 1985). At each sampling date, two 1-m-long sections of crop row were hand-harvested from each plot. Depending on the treatment, samples were randomly harvested about 2 m from the edge of the plots (to avoid border effects) at locations perpendicular to the irrigation tube or the path of subsoiling. Samples were taken with the middle of each sample centered over the irrigation tube or the location where the subsoiler had passed. Plants were cut about 2 cm above the soil surface and taken to the laboratory where branch length and branch number were determined.

Seed yield and yield components were determined by hand-harvesting four 1-m-long samples from each plot at harvest maturity (Growth Stage R8) in both years. Samples were harvested perpendicular to the irrigation tube or the path of subsoiling, with the middle of each sample centered over the irrigation tube or where the subsoiler had passed. Samples were taken about 2 m from the edge of each plot. The four sections from each plot were grouped and the number of plants (main stems) counted. Branches were separated from the main stem so the yield and yield components on the branch and mainstem fractions could be determined separately. For all plots, the total dry weight of each fraction was determined by drying at 75°C for 48 h and weighing. Pods were removed

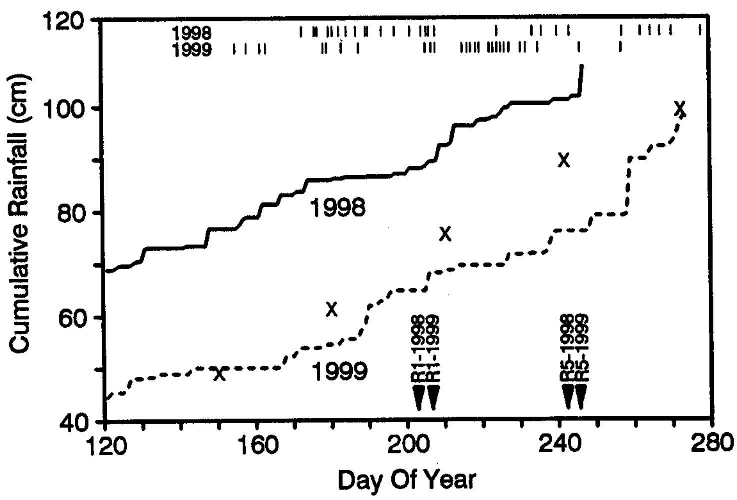

Fig. 1. Cumulative rainfall for the 1998 and 1999 growing seasons. The X symbols indicate normal cumulative rainfall, based on monthly 30-yr. averages (1951–1980). Arrows indicate average date of initial flowering (R1) and beginning of seed fill (R5) over all levels of drought-stress treatment in 1998 and 1999. Vertical lines indicate dates of irrigation in 1998 and 1999.

from the stem material and the dry weight of the vegetative tissue was determined after drying for 48 h. The seed from each fraction was threshed, cleaned, dried at 75°C for 48 h, and weighed. Individual seed weight was determined by counting, drying, and weighing 200 seeds from each fraction. Seed number per square meter was calculated from the seed yield and individual seed weight data. Apparent harvest indices (harvest indices at Growth Stage R8) for the mainstem and branch fractions were calculated by dividing the seed yield of each fraction by its total above-ground dry weight (biological yield). Weather data were collected during the growing season at a weather station located adjacent to the experimental site. Rainfall was above normal in 1998 and near normal in 1999 (Fig. 1). Rate of rainfall accumulation was below normal between Growth Stages R1 and R5 in both years. An extended period without rainfall occurred during seed fill (after Growth Stage R5) in 1998 but not in 1999.

Statistical Analyses

All data collected were analyzed by analysis of variance as a randomized complete block design with four replications. For each variable, a LSD value was calculated to compare differences among levels of drought-stress treatment when the treatment effect was significant at the 0.05 probability level. Pearson correlation coefficients were calculated using the CORR procedure (SAS Institute, 1999) to examine the degree of association between total seed yield and yield from the branch and main stem fractions, between yield of each fraction and the yield components of each fraction, and between branch length and branch number and the yield and yield components from the branches. Correlation analyses were conducted over years using the mean value for each level of drought-stress treatment within each year.

RESULTS AND DISCUSSION

Mainstem Fraction

Drought-stress treatment had no effect on mainstem seed yield in 1998 or 1999 (Table 1). However, the seed yield produced on the mainstem fraction became more important in determining total seed yield the drier the growing conditions (Table 1). Contribution of mainstem seed yield to total seed yield was lowest for the soybean that was irrigated (averaging 34% over both years) and highest for soybean grown with no irrigation or deep tillage (averaging 56%). Soybean grown with irrigation also had the lowest mainstem apparent harvest indices (Table 1), suggesting that the efficiency of seed-yield formation on soybean main stems is increased by drought stress.

Drought-stress treatment had no effect on the number of main stems per square meter at maturity (Table 2). Like mainstem seed yield, there was no effect of drought-stress treatment on mainstem seed number per square meter (Table 2). Mainstem seed yield and mainstem seed number per square meter were positively correlated over both years ($r = 0.835$; $P < 0.05$). In contrast, the correlation between mainstem seed yield and the weight of individual mainstem seeds was not significant ($r = -0.207$). In 1998, the average weight of individual mainstem seeds of soybean receiving irrigation was 15% heavier than the average weight of individual mainstem seeds of soybean grown with no irrigation or deep tillage. However, no treatment differences were found in mainstem individual seed weight in 1999. Less rainfall during seed fill in 1998 than in 1999 (Fig. 1) would explain why the two levels of drought-stress treatment differed in individual seed weight in 1998 but not in 1999. The main stem of determinate soybean generally contributes less to total yield than the branches (Board, 1987; Frederick et al., 1998; Ramseur et al., 1984b). However, our data show that the relative contribution of the mainstem to total seed yield probably depends upon soil water conditions during the growing season.

Branch Fraction

In contrast to the mainstem fraction, drought-stress treatment had a large effect on branch seed yield (Table 3). Averaged over years, branch seed yield of soybean grown with irrigation was 107% higher than the branch seed yield of soybean grown with no irrigation or deep tillage. With respect to drought-stress treatment, the contribution of branch seed yield to total seed yield was the opposite of that found for mainstem seed yield. The percent of total seed yield produced on the branches was highest for the soybean receiving irrigation (average of 66%) and the least for the soybean produced with no irrigation or deep tillage (average of 45%, Table 3). Drought-stress treatment had no effect on the apparent harvest indices of the branches (Table 3), indicating that

Table 1. Soybean mainstem seed yield, contribution of mainstem yield to total yield, and apparent harvest index of mainstem fraction as affected by drought-stress treatment in 1998 and 1999.

Irrigation	Deep tillage	Mainstem seed yield 1998	1999	Percentage of total seed yield on main stems 1998	1999	Mainstem apparent harvest index 1998	1999
		— kg ha^{-1} —		— % —		— kg kg^{-1} —	
Yes	No	1164	1045	38.5a†	29.5a	0.196a	0.192a
No	Yes	1189	1042	53.3b	39.9b	0.238b	0.252b
No	No	1189	1105	68.1c	42.9b	0.232b	0.260b
LSD (0.05)		NS‡	NS	9.6	10.0	0.022	0.060

† Means followed by same letter within a column are not significantly different as determined by Fisher's protected LSD test at P 0.05.
‡ NS = drought-stress treatment effect not significant at the 0.05 probability level.

Table 2. Number of soybean main stems per m^2, mainstem seed number per m^2, and mainstem individual seed weight as affected by drought-stress treatment in 1998 and 1999.

Irrigation	Deep tillage	Number of main stems 1998	1999	Mainstem seed number 1998	1999	Mainstem individual seed weight 1998	1999
		— m^{-2} —		— m^{-2} —		— mg —	
Yes	No	53.8	53.5	673	649	150a†	141
No	Yes	54.8	51.5	754	650	139b	140
No	No	54.3	51.8	791	682	130b	144
LSD (0.05)		NS‡	NS	NS	NS	11	NS

† Means followed by same letter within a column are not significantly different as determined by Fisher's protected LSD test at P 0.05.
‡ NS = drought-stress treatment effect not significant at the 0.05 probability level.

Table 3. Soybean branch seed yield, contribution of branch seed yield to total seed yield, and apparent harvest index of branch fraction as affected by drought-stress treatment in 1998 and 1999.

Irrigation	Deep tillage	Branch seed yield 1998	Branch seed yield 1999	Percent of total seed yield on branches 1998	Percent of total seed yield on branches 1999	Branch apparent harvest index 1998	Branch apparent harvest index 1999
		— kg ha^{-1} —		— % —		— kg kg^{-1} —	
Yes	No	1855a†	2337a	61.5a	70.5a	0.343	0.443
No	Yes	1035b	1566b	46.7b	60.1b	0.306	0.503
No	No	534c	1492b	31.9c	57.1b	0.299	0.466
LSD (0.05)		335	160	9.6	10.0	NS‡	NS

† Means followed by same letter within a column are not significantly different as determined by Fisher's protected LSD test at P 0.05.
‡ NS = drought-stress treatment effect not significant at the 0.05 probability level.

drought stress reduced branch vegetative and reproductive growth proportionally. The increase in branch seed yield with irrigation we found supports previous research by others showing branch seed yield to be more sensitive to unfavorable growing conditions than mainstem seed yield (Board and Harville, 1998; Board and Tan, 1995; Board et al., 1990).

Branch seed number per square meter responses to drought stress were similar to those of branch seed yield (Table 4). Branch seed number per square meter was highly correlated with branch seed yield ($r = 0.994$; $P < 0.0001$) and total seed yield ($r = 0.996$; $P < 0.0001$). The decrease in weight of individual seeds on the branches due to drought-stress treatment was less than the decrease in branch seed number per square meter (Table 4), and the association between branch individual seed weight and branch seed yield was less (0.909; $P < 0.05$) than it was for branch seed number and branch seed yield. Over genotypes and a wide range of growing conditions, seed yield of soybean is usually highly dependent on the number of seeds per unit land area (see review by Frederick and Hesketh, 1994). Our data suggest that decreases in seed yield of determinate soybean due to drought stress between flowering and early seed fill are primarily the result of similar decreases in branch seed number.

Averaged over levels of drought-stress treatments, about 38% of the final number of branches formed on the soybean plants were present at Growth Stage R1 (initial flowering) in 1999, whereas only about 4% of

Table 4. Soybean branch seed number per m² and branch individual seed weight as affected by drought-stress treatment in 1998 and 1999.

Irrigation	Deep tillage	Branch seed number 1998	Branch seed number 1999	Branch individual seed weight 1998	Branch individual seed weight 1999
		— m^{-2} —		— mg —	
Yes	No	1063a†	1432a	152a	153a
No	Yes	554b	927b	145ab	146b
No	No	348b	859b	135b	151ab
LSD0.05		235	401	13	5

† Means followed by same letter within a column are not significantly different as determined by Fisher's protected LSD test at $P \leq 0.05$.

Table 5. Soybean branch length per m² and branch number per m² measured at initial flowering and during seed fill as affected by drought-stress treatment in 1999.

Irrigation	Deep tillage	Branch length R1	Branch length R5	Branch number R1	Branch number R5
		— m m^{-2} —		— no. m^{-3} —	
Yes	No	0.88	40.9a†	54	284a
No	Yes	0.97	17.0b	70	165b
165b					
No	No	1.35	17.0b	106	165b
LSD0.05		NS‡	13.9	NS	68

† Means followed by same letter within a column are not significantly different as determined by Fisher's protected LSD test at $P \leq 0.05$.
‡ NS = drought-stress treatment effect not significantly at the 0.05 probability level.

the final branch length had been obtained by that time (Table 5). Board and Settimi (1986) also reported that most soybean branch vegetative growth occurs after reproductive development begins on the main stem. Drought-stress treatment had no effect on branch number per square meter and branch length per square meter measured at flowering, but had a large effect on the final number and final length of branches formed. Branch seed number per square meter was highly correlated with final branch number per square meter ($r = 0.995$; $P < 0.05$) and final branch length per square meter ($r = 0.994$; $P < 0.05$) in 1999. Branch seed yield was also highly correlated with branch growth ($r = 0.997$; $P < 0.05$ and 0.997; $P < 0.05$ for final branch number and branch length, respectively). This close association between vegetative and reproductive development on the branches would support the similar apparent harvest indices we found for the branch fraction over the three levels of drought-stress treatment (Table 4). Why drought-stress treatment had a large effect on branch yield but no effect on mainstem yield is not known. Similar relationships branch and total seed yield have also been found for determinate soybean in response to reductions in row width (Board et al., 1990; Board and Harville, 1998). The longer time period for reproductive development on the main stem, compared with branches, may be one reason mainstem yield is less sensitive to stresses.

CONCLUSIONS

Drought-stress treatment had its greatest effect on branch vegetative and reproductive development, compared with mainstem development. Testing soybean cultivars and different planting dates, others have also found total seed yield of determinate soybean to be primarily determined by the seed yield on branches (Board, 1987; Board et al., 1990). The close correlation we found between branch vegetative growth and branch seed yield, and the similar branch apparent harvest indices over all levels of drought-stress treatment, indicate that good branch vegetative growth is essential for high seed yields in determinate soybean cultivars grown on the Coastal Plain. Reductions in source strength that cause decreases in crop growth rate between Growth Stages R1 and R 5 have been found to result in decreases in pod and seed number per unit area and, consequently, total seed yield (Board and Harville, 1998; Board and Tan, 1995). This is the period of development when most branch growth occurs (Table 5, Board and Settimi, 1986). These results and our data suggest drought stress occurring between flowering and early seed fill reduces soybean seed yield primarily by reducing branch vegetative growth, which results in fewer branch seeds and less branch seed yield.

Planting soybean late results in less branch vegetative growth, lower branch yields, and lower total yield per plant, which can usually be compensated for by planting at a higher seeding rate in a more narrower row-width configuration (Board, 1990; Ramzeur et al., 1984a; Frederick et al., 1998). In contrast, branch seed-yield reductions due to drought stress probably can not be compensated for by planting at a higher plant seeding rate in narrow rows because of the greater evapotranspiration and severity of drought stress that can occur with narrow row culture (Frederick et al., 1998). Under such conditions, more severe drought stress would probably result in further reductions in branch and, therefore, total seed yield. In contrast to branch seed yield, we found drought-stress treatment to have no effect on mainstem seed yield. Therefore, cultivars having a higher mainstem yield potential (total seed yield less reliant on branch seed yield) than currently recommended cultivars may be more suited to areas where severe drought stress frequently occurs, especially if grown in narrow row culture at higher plant populations.

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